Temperature Effects on Swimming Performance of Larval and Juvenile Colorado Squawfish: Implications for Survival and Species Recovery

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Abstract.—We determined prolonged swimming ability of larval and juvenile Colorado squawfish *Ptychocheilus lucius* at 10, 14, and 20°C. Fatigue velocity (velocity at which 50% of the fish failed to sustain swimming in 30-min tests) increased significantly with water temperature and fish length. Differences in swimming ability between 10 and 14°C became less pronounced as fish length increased, but differences remained substantial between the two cooler and the 20°C swimming experiments for all size-classes tested. We conclude that cold hypolimnetic releases from hydroelectric dams can significantly reduce prolonged swimming ability of young-of-year Colorado squawfish, and may help explain the decline of this species in the Colorado River basin.

The federally endangered Colorado squawfish *Ptychocheilus lucius* is one of several native, large-bodied Colorado River basin fishes currently threatened with extinction. The species was once common in major rivers throughout the basin (Girard 1856; Evermann and Rutter 1895; Miller 1961) but was extirpated from the lower basin (downstream from Glen Canyon Dam, Arizona) by the 1970s (Minckley 1973; Moyle 1976; Minckley 1985); populations in the upper basin suffered widespread declines this century but remain extant (Holden and Stalnaker 1975; Tyus et al. 1987; Tyus 1991). Loss of habitat and migration corridors, along with water depletions, altered flow regimes, and reduced water temperatures—all resulting from hydroelectric dam construction—are primary causes of the species' demise (Minckley 1973; Hickman 1983; Tyus 1991).

Depression of spring–summer water temperatures in dam tailwaters has affected most life stages of Colorado squawfish and other native fishes. Effects of low temperatures include inhibition of spawning (Holden and Stalnaker 1975; Minckley 1991), retardation or cessation of embryonic development (Marsh 1985), and reduction of growth (Black and Bulkley 1985; Thompson et al. 1991), condition, and lipid stores of later life stages (Kaeding et al. 1986; Kaeding and Osmundson 1988). Knowledge of responses of Colorado squawfish and other native fishes to environmental factors is needed for evaluating stream flow recommendations (Maddux et al. 1987; Tyus and Karp 1989; Stanford 1994) and proposals to alter

the temperature of dam effluents (USNPS 1977). If repatriation efforts are to be successful, life history needs must be known so that stocking sites with appropriate environmental conditions can be chosen (Tyus 1991). Laboratory studies concerned with effects of temperature on survival and growth (e.g., Black and Bulkley 1985; Marsh 1985) are in demand.

We examined the effects of temperature on swimming performance of early life stages of Colorado squawfish. Selected experimental temperatures (10, 14, and 20°C) are typical of spring–summer water temperatures in the modified Colorado River and its major tributaries. Temperatures approximate 10°C in major dam tailwaters during the spring–summer reproductive period. Mainstem and tributary river segments unaffected by impoundments exhibit temperatures near 20°C during and following spring–summer spawning. We chose 14°C to represent tailwater–tributary mixing zones and eddy return channels ("backwaters") within tailraces that may warm above main-channel temperatures. The latter habitats are especially important rearing sites for early life stages of Colorado squawfish and other native species in major rivers of the basin (Valdez and Wick 1981; Tyus and Karp 1989).

Tests of swimming performance can provide information relevant to feeding rates (Blaxter 1986; Meng 1993), predation susceptibility (Coutant et al. 1974), and, when combined with flow data, the ability of fish to maintain position in preferred habitats (Harvey 1987). These tests can also be used to evaluate the effect of environmental variables (e.g., temperature) on the swimming performance of fishes (Houde 1969; Griffiths and Al-

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derdice 1972; Beamish 1981; Bernatchez and Dodson 1985). The objectives of our study were to measure the swimming performance of larval, young juvenile, and older juvenile Colorado squawfish at three temperatures, and to evaluate possible effects of body shape (length, weight, and cross-sectional diameter) on swimming performance of young juveniles. Our study was motivated by the possibility that low temperatures and fluctuating flows in dam tailwaters in the Colorado River basin adversely affect swimming performances of larval and juvenile Colorado squawfish, and we discuss how these factors may affect recovery and repatriation efforts on behalf of the species.

Methods

Colorado squawfish were spawned on 1 June and hatched on 7 June 1994 at Bubbling Ponds State Fish Hatchery, Page Springs, Arizona. Approximately 1,000 swim-up fry were moved to a 114-L aquarium held at an ambient room temperature of 20°C. Fish were fed ad libitum five times each day at 2-h intervals with a combination of *Artemia salina* nauplii and Biokyowa® B-250 larval fish diet. At 6 weeks of age, fish were shifted to Silvercup® trout diet. The photoperiod was 8–9 h light:15–16 h darkness; artificial light was supplemented by natural light passed by windows in all but the north wall of the laboratory. Fish were acclimated from 20°C water to 10 and 14°C water for at least 4 d before experiments.

Fatigue velocity (FV50) is the velocity at which half the fish fail to maintain swimming; it is measured by subjecting fish to velocity increments within the range of swimming abilities (for larval fishes, see Houde 1969, Laurence 1972, and Meng 1993; for adult fishes, see Brett 1967, Farlinger and Beamish 1977, Berry and Pimentel 1985, and Mesa and Olson 1993). Tests are run for a predetermined amount of time (30 to 200 min) at a constant water velocity. Dichotomous pass–fail data are recorded and analyzed with bioassay techniques (Brett 1967; Houde 1969; Bernatchez and Dodson 1985). We used this method because studies involving larval fish have shown a tendency for swim times to be bimodal (Houde 1969; Meng 1993) and for extremely high variation among individual larvae (Houde 1969). The pass–fail FV50 method provides a good measure of mean swimming performance, despite such variation (Brett 1967).

We measured swimming performance of larval and juvenile Colorado squawfish by determining FV50 values during 30-min tests at three temperatures. Larval fish (13.0–14.1 mm mean total length, TL; 26–37 d posthatch) were exposed to incremental test velocities from 9.3 to 18.4 cm/s, and young juvenile fish (21.5–22.3 mm mean TL, 65–78 d old) were tested at velocities from 12.4 to 19.4 cm/s. Older juveniles (27.7–28.8 mm mean TL, 105–116 d old) were exposed to velocities ranging from 12.4 to 22.8 cm/s. At least five fish were tested at each velocity, and fish were subjected to at least three velocities (encompassing the range of swimming ability) at each temperature.

The swim tube employed, while borrowing from the design of Houde (1969) and Meng (1993), differed from others in that water was driven by means of a pump, rather than by gravity flow. The tube consisted of a 75-cm section of clear, 25.4-mm polyvinyl chloride (PVC) pipe connected upstream to either a 3.8- or 37.8-L/min flowmeter (Eager, Inc.®) or a combination of the two (Figure 1). Water was pumped through the 37.8-L/min flowmeter by a 1/40-horsepower (hp) electric pump and through the 3.8-L/min flowmeter with a 1,900-L/h pump, which also pumped water to a source reservoir consisting of a series of six 37.8-L aquaria. Water pumped to and from the swim tube was carried in clear 25- and 19-mm flex tubes, respectively. Water temperature was maintained within ±0.5°C by ambient temperature at 20°C and by Aquanetics® 1/4-hp chillers for 14 and 10°C experiments.

Fish were inserted in the test system after the following steps: the swim tube was filled with water at the acclimation temperature, flow was stopped by valves on the flowmeters, the ball valve was closed at the downstream end, and the tube was pulled apart at the upstream slip coupling. Following reassembly, flow was resumed by reopening the downstream ball valve and upstream needle valve, and air was removed by raising the downstream end and allowing current to flow at a predetermined acclimation velocity. Fish were held in the transparent portion of the tube by blocking the upstream and downstream ends with nylon screening.

We calibrated flowmeters for mean velocity by timing passage of dye through the swim tube at different flowmeter settings; 10 calibration tests were performed for each setting. Dye was injected with a 16-gauge hypodermic syringe fitted through a hole drilled in the PVC piping.

We tested larvae and older juveniles in pairs; young juveniles were tested individually. Single-
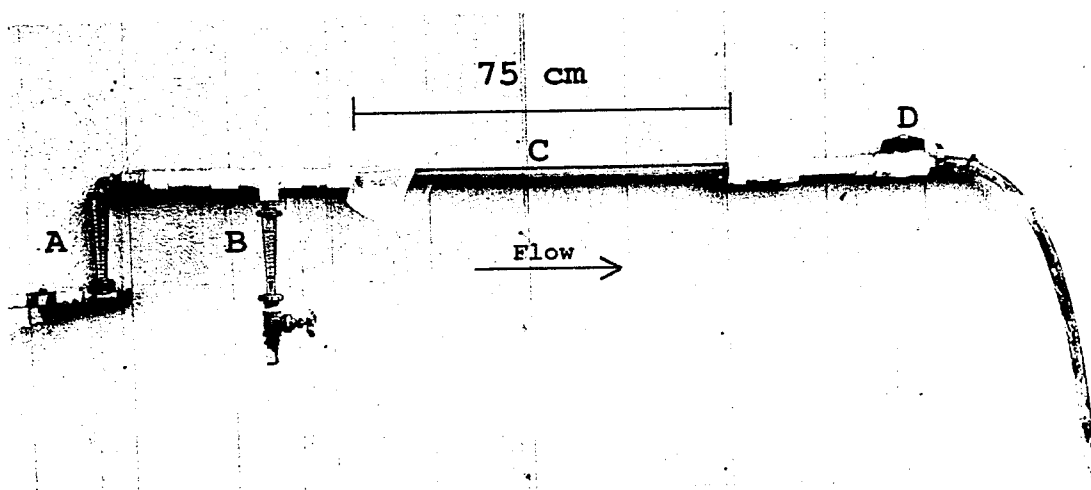
FIGURE 1.—Swimming apparatus used to determine the swimming ability of larval and juvenile Colorado squawfish. The swim tube was 75 cm long and constructed of clear, 25-mm polyvinyl chloride pipe. Objects in the figure are labeled as follows: A: 3.8-L/min flowmeter; B: 37.8-L/min flowmeter; C: swim tube; D: downstream ball valve.

fish trials were necessary to evaluate the effects of length, weight, and cross-sectional diameter on individual swimming ability for young juveniles because results for paired fish (larval and older juvenile tests) could not always be uniquely attributed to individuals. We were concerned that small differences in morphology might be accompanied by relatively large differences in swimming performance.

Following their insertion into the tube, fish were exposed to a velocity of 0.5 times test velocity and allowed to acclimate for 10 min. Fish were coaxed to swim by placing a 30-cm length of styrofoam over the top of the tube for cover, and agitating the tube at the downstream end until swimming commenced. All fish that failed to swim during acclimation were excluded. Following acclimation, fish that successfully swam for 30 min were scored as "passed," whereas fish that were pinned against the downstream screen for more than 1 min during a test "failed," and "fatigue time" (the time swimming ceased) was recorded. Fish were then euthanized in MS-222 (tricaine methanesulfonate) and placed in 10% formalin. Total lengths and weights were recorded, and cross-sectional diameter was measured for both size-classes of juveniles. Blocking forces (Bell and Terhune 1970; Webb 1975) were probably insignificant because none of the fish had a cross-sectional area greater than 10% of that of the swim tube.

Fatigue velocities and their confidence intervals were calculated for each temperature via probit analysis (Finney 1971) for nonaggregated data

(SPSS 1992). Pearson's test of independence (Sokal and Rohlf 1981) was used to test for possible relationships between acclimation temperature and the rate at which acclimation was completed. We examined the effect of length, weight, and cross-sectional diameter on swimming ability of young juveniles using one-way analysis of variance. Although preliminary observations indicated no behavioral differences between fishes tested individually (young juveniles) and those tested in pairs (larvae and older juveniles), we cannot rule out the possibility that pairing of fish influenced results. All size-classes were included in analyses, however, because we were primarily interested in the effect of water temperature on swimming ability within each size-class, and all fish within each size-class were tested identically. Presence of significant social effects in the paired-fish swimming trials (larvae and older juveniles) would confound comparisons of swimming performance between these size-classes and the young juveniles, so no such statistical comparisons were made.

Results

Analysis-of-variance of young juvenile Colorado squawfish (range, 19.3–24.4 mm TL; Table 1) revealed no significant effects of length, weight, or cross-sectional diameter on response (pass, fail, or failure to swim during acclimation) of individuals ($P > 0.26$ in all tests). Based on these results, we conclude that variation in body shape likely had no significant effect on swimming response within the young juvenile size-class. We assumed

TABLE 1.—Prolonged swimming ability of larval and juvenile Colorado squawfish. Fatigue velocity values (FV50) at 30 min are expressed in centimeters per second (cm/s) and body lengths per second (BL/s); 95% confidence limits (CI) are shown in parentheses.

| Temperature, C°	Total length, mm		Number of velocities tested	Number of fish	FV50, cm/s (CI)	FV50, BL/s (CI)
	Mean ± SD	Range				
			Larval Colorado squawfish			
10	14.1 ± 0.5	12.5–15.0	3	21	10.5 (9.9–11.1)	7.4 (7.0–7.9)
14	13.4 ± 0.4	12.5–14.3	3	20	13.5 (12.8–14.2)	10.1 (9.5–10.6)
20	13.0 ± 0.6	11.3–14.3	5	50	16.1 (15.6–16.6)	12.4 (12.0–12.8)
			Young juvenile Colorado squawfish			
10	22.3 ± 1.2	20.5–24.4	3	15	13.3 (12.4–14.2)	6.0 (5.6–6.4)
14	21.5 ± 1.2	19.3–23.4	4	20	14.7 (13.8–15.6)	6.8 (6.4–7.2)
20	21.7 ± 1.2	19.8–24.1	4	20	17.4 (16.5–18.4)	8.0 (7.6–8.5)
			Older juvenile Colorado squawfish			
10	28.4 ± 1.5	25.2–32.1	5	33	14.2 (13.3–15.1)	5.0 (4.7–5.3)
14	28.8 ± 1.8	23.8–33.4	5	38	15.2 (14.4–16.1)	5.3 (5.0–5.6)
20	27.7 ± 1.7	24.4–30.8	4	48	19.2 (18.3–20.1)	6.9 (6.6–7.2)
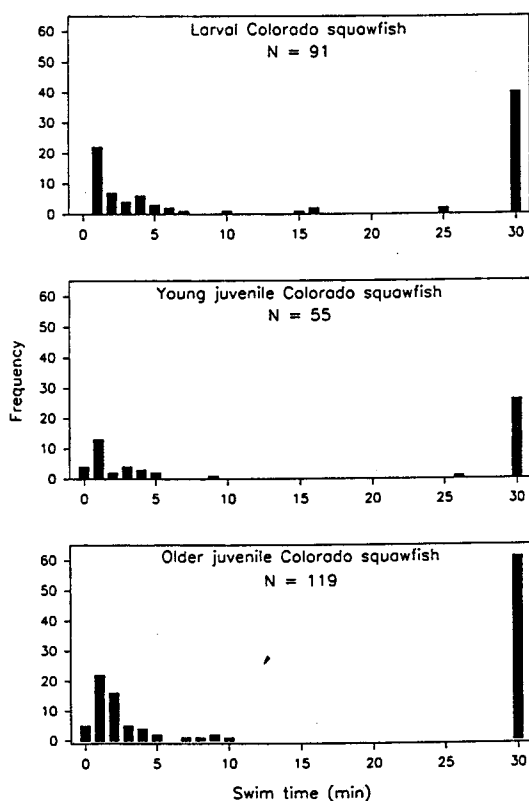
FIGURE 2.—Frequency distributions of swimming times for mesolarval, young juvenile, and older juvenile size-classes of Colorado squawfish during fatigue velocity (FV50) tests.

that responses of the young juveniles were representative of responses within the larval and older juvenile classes as well.

Pearson chi-square tests indicated that all data fit the probit model for each size-class and temperature ($P > 0.33$ for all tests), and FV50s and their confidence limits were calculated (Table 1). Response times for individuals were bimodal: most fish either failed in the first 5 min or successfully completed the 30-min tests (Figure 2). Fish that failed usually struggled for at least 1 min at the downstream end of the swim tube in an apparent effort to avoid becoming pinned against the nylon screening.

Absolute FV50 values, expressed in cm/s, increased with both temperature and size-class (Table 1; Figure 3). The FV50s of both larvae and young juveniles differed significantly among the three test temperatures ($P < 0.05$) as determined by tests of relative median potency in the probit procedure (SPSS 1992). Absolute swimming speeds of older juveniles also differed significantly among test temperatures, except that FV50 values were similar at 10 and 14°C (Figure 3). At each temperature, FV50 values differed significantly ($P < 0.05$) between larvae and older juveniles, indicating increased swimming ability with length.

Fatigue velocity values expressed in body lengths/s (BL/s, Table 1) showed a reciprocal trend: larvae exhibited the highest relative swimming abilities (7.4–12.4 BL/s) and older juveniles the lowest (5.0–7.0 BL/s). Relative swimming ability also increased with temperature for each group.

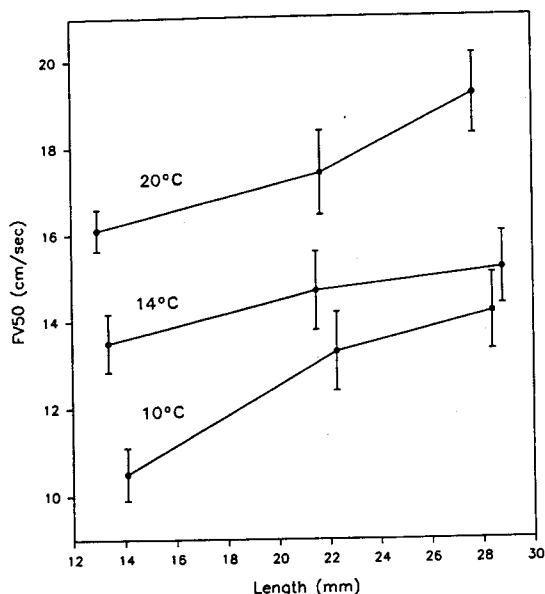Failure to swim during acclimation was strongly

FIGURE 3.—Relationship between fatigue velocity values (FV50, cm/s), water temperature, and length of young Colorado squawfish. Vertical brackets indicate 95% confidence limits for the FV50 values.

associated with lower temperatures for two of the three groups studied (Pearson chi-square, $P <$ 0.001, $P = 0.12$, and $P < 0.001$, for larvae, young juveniles, and older juveniles, respectively). All fish appeared less motivated to swim at colder temperatures; only 2 of 121 fish failed to swim during acclimation in 20°C tests, but 32 of 101 fish at 10°C and 26 of 104 fish at 14°C did not swim. Lack of a significant association with temperature for young juveniles may have been an artifact of sample size; 19 larvae (17%), 11 young juveniles (17%), and 30 older juveniles (20%) failed to swim during acclimation.

All fish that began swimming chose to swim beneath the styrofoam cover both during and after acclimation. This response differs from that reported for larval striped bass *Morone saxatilis* (Meng 1993), which showed a strong proclivity for lighted portions of the tube. In our study, fish may have used the darkened portion for orientation, because no other visual cues were provided.

Discussion

Prolonged swimming ability of larval and juvenile Colorado squawfish was significantly reduced by a decrease in temperature from 20°C to either 14 or 10°C. Swimming ability was also reduced when temperature was decreased from 14°C

to 10°C, but the effect was less pronounced as fish size increased. Although swimming ability increased with temperature, we did not reach the asymptote for peak swimming performance, which, based upon the temperature preferenda established by Bulkley et al. (1981), likely would have occurred near 25°C. Approaching this maximum was not our goal, however, as we were trying to reproduce temperature conditions typical during the spring–summer periods of Colorado squawfish reproduction and rearing in the Colorado River basin.

Similarly, we did not reach the asymptote for peak relative swimming ability (measured in BL/s) of Colorado squawfish. This measure of swimming ability usually reaches its maximum value in smaller (larval) fish and decreases as fish length increases (Beamish 1978). The FV50 value of 12.4 BL/s for larval Colorado squawfish at 20°C is, to our knowledge, higher than others reported for this length of fish (13–15 mm TL), although values approaching this are known (Larimore and Duever 1968; Beamish 1981). The pre-anal fin fold was prominent in larval squawfish tested, but all fins except the pelvics were highly developed as well. Thus, although still in the mesolarval stage (Snyder 1981), the small fish were relatively well equipped for swimming. We are confident in the high value of relative swimming ability because our FV50 values in BL/s quickly approached commonly reported levels for other fishes (reviewed by Bulkley et al. 1981, Berry and Pimentel 1985, and Meng 1993) as fish length increased (Table 1).

The 30-min trials were shorter than many reported in the literature, and probably resulted in higher FV50 values than would have been obtained in longer endurance tests. Studies of sockeye salmon *Oncorhynchus nerka* (Brett 1967) and chars *Salvelinus* spp. (Beamish 1980) indicate that sustained swimming speeds of larger fish (>100 mm) are roughly 80% of the FV50 values obtained in 30-min tests. Use of unexercised fish in our swimming trials, however, probably resulted in a downward bias to our data (Webb 1975; Young and Cech 1993). In any case, the dependency of relative swimming ability upon fish size (Brett 1967; Bernatchez and Dodson 1985) and developmental stage (Houde 1969) makes interspecific comparisons of larval and juvenile fishes problematic.

Large reductions in relative swimming ability of larval (40%), young juvenile (25%), and older juvenile (28%) Colorado squawfish when temperature dropped from 20 to 10°C (Table 1) and strong associations between lower temperature and fail-

ure to swim during 10-min acclimation periods may have important adaptive consequences for wild fish. Spawning of Colorado squawfish presumably occurred in response to decreasing flow (Nesler et al. 1988) and rising water temperature (Minckley 1973; Tyus 1991), thus exposing larval and early juvenile offspring to the warmest water temperatures of the year. Currently, hypolimnial releases from major dams (e.g., Flaming Gorge Dam, Glen Canyon Dam) seldom exceed 14°C (Vanicek and Kramer 1969; Vanicek et al. 1970; Maddux et al. 1987). Even if larval and juvenile Colorado squawfish manage to develop and survive in cold tailwater temperatures (or survive cold shock when drifting from warm tributaries into cold tailwater reaches: Berry 1988; M. R. Childs, unpublished data) and find areas of low current velocity in which to reside, they still must overcome a reduced ability to search for food (Blaxter 1986) and an increase in predation loss (Coutant et al. 1974) because of their reduced swimming ability. They must also overcome effects of reduced growth rates (Black and Bulkley 1985), including increased early life mortality and decreased survival to sexual maturity (Kaeding and Osmundson 1988). These negative effects are attributable to reduction of water temperatures below historical norms in combination with altered flow regimes.

Swimming performance is fairly consistent across a wide variety of fish species when compared on the basis of equal length and within an individual's range of thermal tolerance (Beamish 1981). Native Colorado River fishes all exhibit similar thermal temperature preferenda (Bulkley et al. 1981), as might be expected of fishes that evolved within the same drainage. A return to natural temperatures below major dams in the Colorado River basin by means of epilimnetic (instead of hypolimnetic) discharges (USNPS 1977; Stanford and Ward 1986; USFWS 1994) should therefore help alleviate some of the negative impacts on native larval and juvenile fish, which are adapted to warmer temperatures in the spring and summer. Such adjustment will also provide hope for repatriation of Colorado squawfish and other rare native fishes. However, failure to provide migration avenues for adult Colorado squawfish, which undergo lengthy spawning migrations (Tyus 1984; but see McAda and Kaeding 1991) and require a variety of habitats for various life stages (Stanford 1994), may preclude recovery for this species in these areas.

Return to the normal temperature regime alone, however, would provide an equally suitable habitat for many introduced warm-water species (Minckley 1991; Stanford 1994) and might therefore be undesirable. Reduction in daily fluctuating discharges from Flaming Gorge and Glen Canyon dams (USFWS 1992, 1994) would allow for greater daytime warming of edgewater nursery habitats (Wick et al. 1983) for the remaining native fishes while also maintaining a cold-water barrier to some introduced fishes. However, without main-channel temperature increases, successful reproduction by native species will remain improbable. As similarly advocated by Meffe (1992) for Pacific coast salmonids, we believe that management and recovery of native Colorado River basin fishes below hydroelectric dams will depend upon adoption of operational schemes that function within constraints of the fishes' life histories, including returns to more natural hydrologic patterns (consisting of temperature, discharge, and sediment transport modifications) and restoration of migration corridors.

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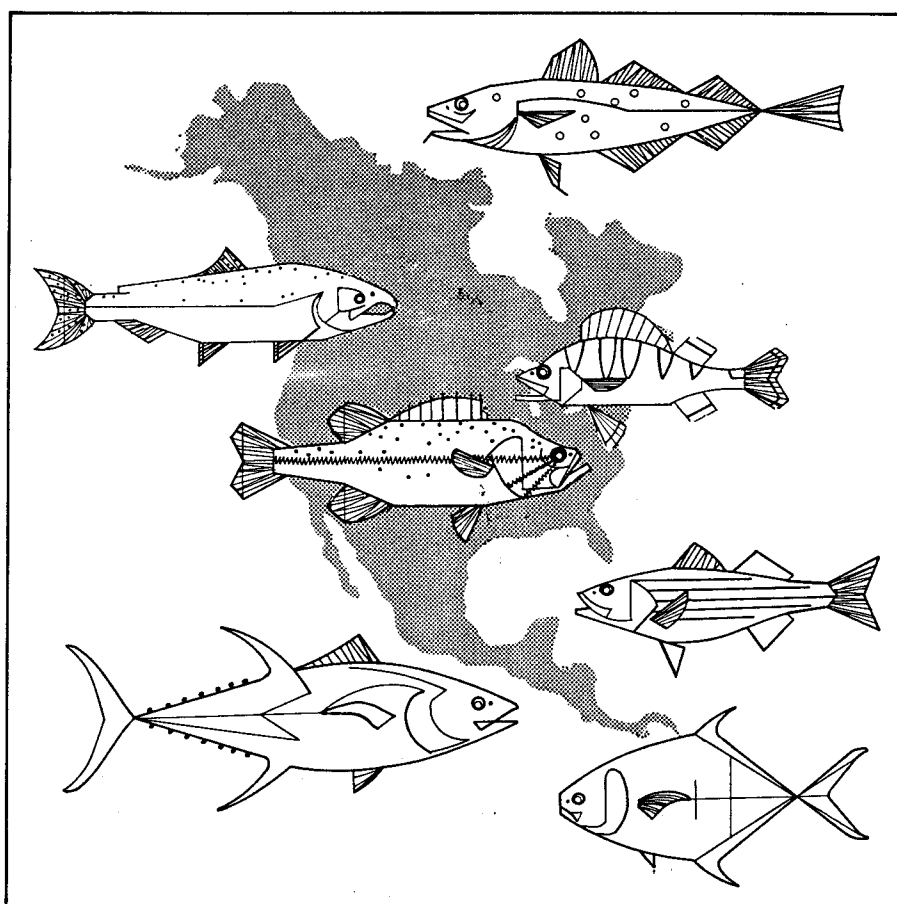
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